A Unique Type of Microsporangium in Selaginella Series Articulatae

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One of the most distinct taxonomic groups in the genus *Selaginella* is the series *Articulatae*, comprised of about 40 taxa endemic to Latin America, one species that is in South Africa, the Azores and Latin America, and several that are restricted to Southeast Asia. This heterophyllous group, first described by Spring (1850) and maintained in later classifications by Hieronymus (1901) and Walton and Alston (1938), takes its name from the articulations located just below each bifurcation of the stem. These appear either as dark-colored swellings in living material or as dark constrictions in some dried specimens. Other morphological characteristics that unify the group are: (1) each strobilus has only a single (or rarely two) basal megasporangia; (2) each enlarged fertile megasporophyll is subtended by one or more enlarged sterile leaves; (3) the megaspores are exceptionally large and have high crestoreticulate muri; (4) the microspores are pale (usually buff to tan) and have ornamentation of sharp spines on their exines; and (5) the aerial roots arise dorsally from the stem. Also, about three-fourths of the taxa in the series have bistelar or multistelar stem anatomy, a feature not found elsewhere in the genus.

During a taxonomic survey of the *Articulatae*, a previously undescribed type of microsporangium was found to be another unifying feature. A survey of nearly all of the articulate taxa and many non-articulate ones supported this generalization. An explanation of the survey and a description of the microsporangia follows.

MATERIALS AND METHODS

Specimens of *Selaginella* with articulate stems from the following herbaria were examined: ENCB, F, FSU, G, GA, GH, H, K, MO, NY, P, PR, PRC, TENN, UC, UMEX, UPS, US and VT. A comprehensive survey of other *Selaginella* taxa was not undertaken, but representatives of many non-articulate taxa were examined during the course of the study.

The basic structural differences between articulate and non-articulate microsporangia were discernable to the naked eye, but in order to see anatomical details, slides were prepared using Hoyer's solution (Anderson, 1954). For even closer scrutiny, a few microsporangia were examined with a scanning electron microscope. Initially an AMR model 900 SEM was used, but later an ETEC autoscan model U-1 was employed. Samples were mounted on standard aluminum studs (Ladd Research Industries) using air-drying silver conductive paint (GC Electronics) or double-faced cellulose tape. The prepared studs were coated with vaporized carbon and gold in a Denton model 515 vacuum-coater with a randomly rotating head.

RESULTS AND DISCUSSION

The microsporangia of typical non-articulate *Selaginella* are simple, bivalved structures. They are hinged at the base and split open along a lateral suture which runs from the apex down each side of the sporangium, forming two equal halves

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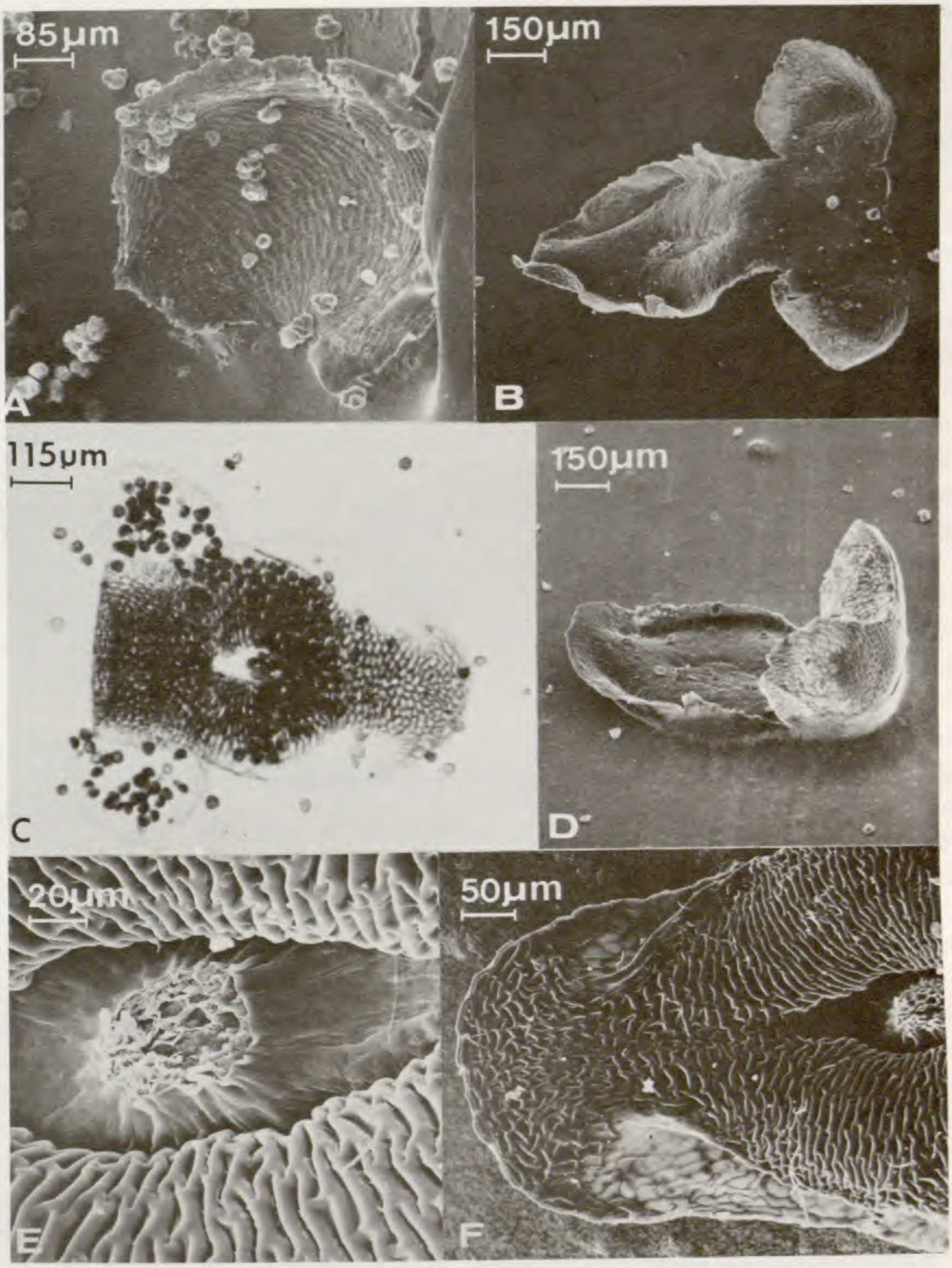

FIG. 1. Features of open microsporangia in non-articulate and articulate species of *Selaginella*. FIG. A. One valve from microsporangium of non-articulate *S. oaxacana* (*Evans & Bowers 3223*, TENN). FIG. B. SEM view of completely opened microsporangium from *S. subarborescens* (*Hermann 11221*, US). FIG. C. Open microsporangium of *S. sertata* (*Allen 1959*, GH), with the abaxial end folded under. FIG. D. SEM view of open microsporangium of *S. fragilis* (*Lindeman 4007*, US). FIG. E. SEM view of basal portion of microsporangium of *S. fragilis* (*Lindeman 4007*, US) showing bands of annuloid cells on either side of sporangial stalk. FIG. F. SEM view of portion of microsporangium of *S. fragilis* (*Lindeman 4007*, US) showing annuloid bands of cells around sporangial stalk and cells forming suture line of dehiscence.

upon dehiscence. Each half is nearly hemispherical and consists of uniform cells (*Fig. 1A*). According to Goebel (1901), microsporangial cell walls in *S. flabellata* Spring, a non-articulate species, are differentially thickened, being thinner on their outer walls than on their inner tangential and radial walls. He described and illustrated microsporangia from a number of species, none of them articulate. Steinbrinck (1902) considered microsporangia to be much simpler in design than megasporangia; he described the former as "primitive" and "of unartistic origin." He based his judgement on material labeled *S. flabellata* sent to him by Goebel.

Microsporangia of the articulate species of *Selaginella* are more complex than those of non-articulate ones. They possess two distinct tissue types. At the base of each sporangium are two broad bands of relatively thick-walled cells. These bands converge on both sides of the short sporangial stalk (*Figs. 1C, E, F* and *2A, B, E*) and continue as broad annuloid bands up the curved faces of the sporangium. The adaxial and abaxial sides of the sporangia are not identical. Dehiscence occurs along a distinct suture line that leaves a tongue-shaped segment on the adaxial side and a larger, two-lobed portion, representing the remainder of the sporangium (*Fig. 1B-D, F*), on the abaxial side. The two lobes, which were the radial faces of the sporangium, are composed of flat, thin-walled cells (*Figs. 1B, D, F* and *2C, D*). These lobes remain concave on their inner faces and often carry masses of microspores upwards during dehiscence.

Goebel (1901) and Steinbrinck (1902) found that both mega- and microsporangia possessed cells with thick walls except on their outer faces. Goebel was uncertain about how the sporangia dehisced, but Steinbrinck strongly advocated the idea that cohesive forces of water played a major role. To support his hypothesis, Steinbrinck placed ripe megasporangia in absolute alcohol for 24 hours, and then dried them out in the air. Dehiscence did not occur. Then he placed the same sporangia in water until the cell lumina were filled with water. When they were allowed to dry the second time, they dehisced normally, demonstrating the importance of water in the dehiscence mechanism.

The same principles of cohesion and adhesion probably apply to the dehiscence of the unique microsporangia of the articulate species of *Selaginella*. When these microsporangia are immersed in water, they remain round and turgid; but when removed and allowed to dry, they gradually open. A combination of cohesive and adhesive forces during desiccation may cause the outer tangential walls of the cells in the thick walled regions to be pulled inward (*Fig. 1E*), thus causing tension along the suture line and the subsequent curling back of both ends of the banded region. My observations of excised microsporangia, when removed from water, show that they may curl completely inside out upon drying.

The annuloid banding is somewhat different than in ferns. A cross-sectional view through a microsporangium of *S. atirrensis* Hieron. (*Fig. 2A, B*) reveals that the cells are higher in the center of each band and taper in size laterally. Also, in this particular example the radial and inner tangential walls of the cells do not appear noticeably thicker than the outer tangential walls. In these respects they resemble the bulliform or "motor" cells described by Esau (1953, p. 145) as epidermal features of certain grasses that curl or fold their leaf blades.

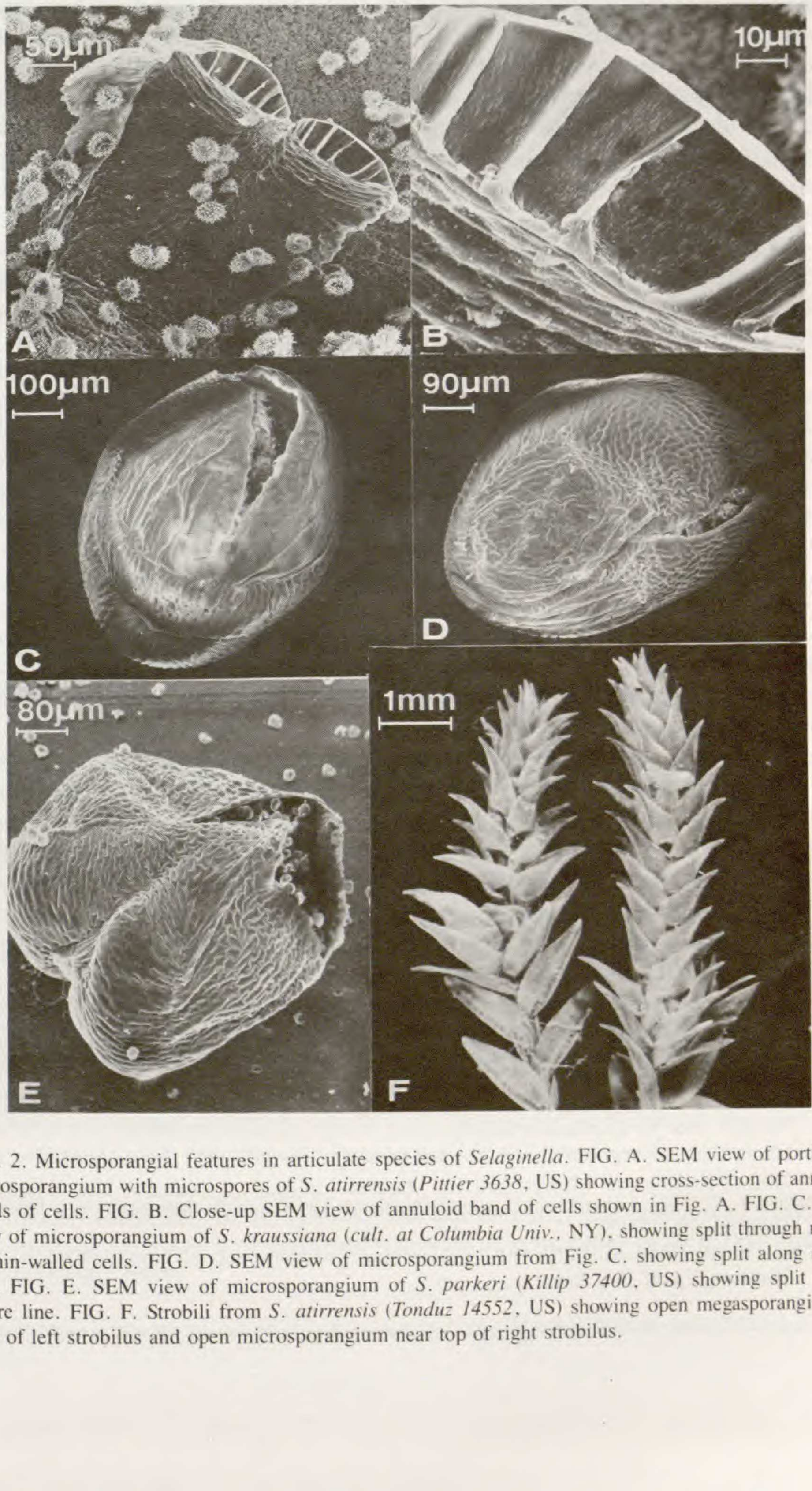

FIG. 2. Microsporangial features in articulate species of *Selaginella*. FIG. A. SEM view of portion of microsporangium with microspores of *S. atirrensis* (*Pittier 3638*, US) showing cross-section of annuloid bands of cells. FIG. B. Close-up SEM view of annuloid band of cells shown in Fig. A. FIG. C. SEM view of microsporangium of *S. kraussiana* (*cult. at Columbia Univ.*, NY), showing split through region of thin-walled cells. FIG. D. SEM view of microsporangium from Fig. C. showing split along suture line. FIG. E. SEM view of microsporangium of *S. parkeri* (*Killip 37400*, US) showing split along suture line. FIG. F. Strobili from *S. atirrensis* (*Tonduz 14552*, US) showing open megasporangium at base of left strobilus and open microsporangium near top of right strobilus.

The opening of the microsporangium is not accompanied by a sudden recoiling of the annulus and catapulting of the spores. Instead, it breaks first at the apex along the suture line and then continues gradually downward along the border between the annuloid bands and the pockets of thin-walled cells. Each microsporangium is oriented so that its longer axis, with its pockets of thin-walled cells, is situated outwardly against the subtending sporophyll. When dehiscence occurs, the force of the uncurling annuloid bands may be exerted against the appressed sporophyll, forcing it downward. As the sporangium continues to curl back, it becomes exserted from the sporophyll (*Fig. 2F*), exposing the two concave lobes containing micro-spores. At this time the spores can be picked up by the wind, splashed away by rain, or washed down the sides of the strobilus, possibly into an open megasporangium at its base.

In summary, the *Articulatae* possess a type of microsporangium not found elsewhere in the genus and considered to be more advanced evolutionarily because of the presence of annuloid bands of cells that probably facilitate dehiscence. Unlike the explosive dehiscence in sporangia of ferns, the microsporangia of the *Articulatae* just slowly uncurl, breaking along a defined suture line of border cells and gradually lifting the masses of spores upward. While a hygroscopic mechanism is obviously responsible for dehiscence, the anatomical and physiological details are yet to be described.

The discovery of this unique and highly developed type of microsporangium within the *Articulatae* makes it more apparent than ever that the group is a well defined taxonomic unit within *Selaginella*. Combined with the other characteristics noted above, it can be argued that the group should be elevated to a subgenus. Existing classifications recognize 2–4 subgenera. Hieronymus (1901) split the genus into the homophyllous and heterophyllous taxa, and Walton and Alston (1938) followed Baker's (1887) basic classification, where the heterophyllous taxa were subdivided into three groups based mainly on whether the sporophylls were uniform or dimorphic. If one assumes equal weighting of taxonomic characters, the *Articulatae* should have, at least, as high a rank as any of the traditional subgenera.

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